

## SPATIAL DISTRIBUTION PATTERNS OF *TILLANDSIA VIOLACEA* (BROMELIACEAE) AND SUPPORT TREES IN AN ALTITUDINAL GRADIENT FROM A TEMPERATE FOREST IN CENTRAL MEXICO

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**ABSTRACT.** The spatial distribution pattern of *Tillandsia violacea* Baker was studied along an altitudinal gradient in a temperate forest in “El Chico” National Park, Hidalgo, Mexico, with emphasis on the host tree species. Results clearly showed a clumped spatial distribution pattern in the four habitat types of host trees. We found a positive effect of altitude in the *T. violacea* abundance, a preference for *Abies religiosa* as host tree, and a relation between height of host trees and abundance of *T. violacea*.

**Key words:** Epiphytes, bromeliads, altitudinal variation, “El Chico” National Park, temperate forest, Mexico

**RESUMEN.** Se estudió el patrón de distribución espacial de *Tillandsia violacea* Baker en un gradiente altitudinal en un bosque templado en el Parque Nacional “El Chico,” Hidalgo, México, con énfasis en la especie de árbol soporte. Nuestros resultados mostraron un patrón de distribución claramente agregado en los cuatro tipos de hábitat en el árbol soporte. Se encontró un efecto positivo de la altitud sobre la abundancia de *T. violacea*, y una tendencia de estas plantas a usar preferentemente *Abies religiosa* como árbol soporte. También se encontró una relación significativa entre la altura del árbol soporte y la abundancia de epífitas.

**Palabras clave:** Epífitas, bromeliads, variación altitudinal, Parque Nacional “El Chico,” bosque templado, México

### INTRODUCTION

Temporal and spatial patterns of distribution allow an understanding of the changes in epiphyte populations and the factors responsible for the patterns. Determination of spatial and temporal patterns in epiphytic plants involves technical problems such as access to the plants (Hazen 1966, Madison 1979, García-Franco & Peters 1987). Differentiation between individuals can be a problem, because many epiphytic species grow and reproduce (sexually and asexually) in clumps (Benzing 1990). Although a number of studies concerning spatial distribution have been developed in greenhouses and cultivated fields (e.g., Yeaton & Gladstone 1982,

Catling et al. 1986), only a few studies have been conducted in the natural environment (García-Franco & Peters 1987, Bøgh 1992, Freiberg 1996, Nieder et al. 2000). Studies have been carried out on single trees (Yeaton & Gladstone 1982), in transects into the forest stands (Tremblay 1997), and in tree stands (Hietz-Seifert et al. 1996). Their results, however, are not easy to compare because they used different methods and scales to explain the same phenomena.

Many factors are involved in the distribution of vascular epiphytes. Using a base data analysis of the epiphytic vegetation, Oksanen (1988) found in Finland that the microclimate (specific site on the host trees) is the main factor affecting spatial distribution. Possibly this was a result of variations in transpiration and evaporation rates

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and different angles of radiant light on the trunk, branches, and treetops (Fitzjarrauld & Moore 1995). Another key factor is surrounding vegetation, which influences water and nutrient availability to the epiphytes. Finally, host trees and their architecture may offer a variety and type of substratum favorable to epiphyte establishment.

Most studies concerning epiphytic distribution have focused on the host tree (phorophyte) as the sampling unit. Host characteristics such as age and size are crucial to epiphytic presence (Zotz et al. 1999). Vandunné (2002) found in a secondary forest in Colombia that the spatial distribution of bromeliads was determined by the availability of branches for establishment, the proximity of conspecific specimens, and the landscape geomorphology. In addition, he found that surrounding vegetation affected the position of epiphytes on the phorophytes.

The altitudinal gradient in the presence of plants has been explained in relation to habitat heterogeneity and substratum fertility (Givnish 1999). Some studies have shown general patterns in which species richness decreases in relation to the increase in altitude (Cowling & Samways 1994, Leathwick et al. 1998). Exceptions exist, however, such as with epiphytic plants in tropical forests of South America, where the tendency is the opposite (Ibisch et al. 1996). Pioneer studies on the relationship between altitude and epiphytic abundance showed that epiphyte density increased with altitude (Gilmartin 1964). Nevertheless in a tropical forest of Mexico, the abundance of *Tillandsia* spp. reduced greatly with altitude (García-Franco & Peters 1987). Reasons for these differences are unclear, but it has been suggested that vegetation composition and nutrient availability can determine the altitudinal distribution and explain species richness (Ohlemüller & Wilson 2000).

Studies on epiphytic spatial distribution, particularly of bromeliads, have been conducted in tropical forest ecosystems, but little information is available on this subject for temperate ecosystems. Spatial distribution of epiphytes within tropical forests is strongly related to structural parameters of host trees (e.g., tree architecture, branch diameter and inclination, substrate, bark texture) and to the canopy microenvironment. Despite differences in various aspects of temperate and tropical forests, we expect that some patterns will be present in both. In this work, we studied the distribution of *Tillandsia violacea* Baker along an altitudinal gradient in a temperate forest in the central part of Mexico, with emphasis on the host tree species.

## MATERIALS AND METHODS

### Study Area

The study was performed in “El Chico” National Park (2739 ha) located north of Pachuca City in Hidalgo State, Mexico (20°13'25"N, 98°45'31"W), at an altitude of 2300–3020 m (Vargas-Márquez 1984). The soils are derived from volcanic rocks (Aguilera 1962). The climate is temperate, humid with cool winters, the annual average temperature is 10° to 14°C (minimum –6° to –9°C), and the annual average precipitation is 1479 mm, with the highest amount in June (240.7 mm) and the lowest in February (18.6 mm), with moderate to high rainfall during fall (Melo & López 1994). The vegetation is temperate forest with stands dominated by the genera *Abies*, *Pinus*, *Cupressus*, *Quercus*, and the shrub *Juniperus monticola* (Rzedowski 1988). The *Abies-Quercus* forest is distributed at altitudes from 2700 to 3000 m (Rzedowski 1988). *Tillandsia violacea* is an abundant epiphyte on *Abies religiosa* and *Quercus* spp. at 2400–3000 m. Other epiphytes, including ferns and mosses, are also common in the same tree species (Medina 1980).

### Spatial Distribution Patterns

During February 1998, this study determined the distribution pattern of *Tillandsia violacea*. Observations were made at an altitudinal gradient of 2700–3000 m in a transect with a 135° SE orientation. Four squares of 15 × 15 m were located along each 100 m in altitude, with the squares separated by 50 m of forest. We recorded all the trees in each square and obtained from each individual tree total height and height between first branch and treetop. A modification of Oschner's tree classification (Braun-Blanquet 1979) was used to divide each tree into four habitat classes: trunk (from base trunk to first branch), tree crown base (first branches section), branches (lower half of the crown), and small branches (upper half of the crown).

Spatial distribution analysis was made with three parameters: (1) Poisson distribution for random frequency in each class; (2) Negative binomial distribution for clumped distribution; and (3) Morisita dispersion index, which is not affected by sample size (Ludwing & Reynolds 1988). To determine the effect of the host tree species, habitat class, and altitude on the *Tillandsia violacea* distribution, we used a X<sup>2</sup> square test (Zar 1984).

### Support Trees Effect

Host tree preference was evaluated during March 1998. In an area of 10,000 m<sup>2</sup> at 2700 m

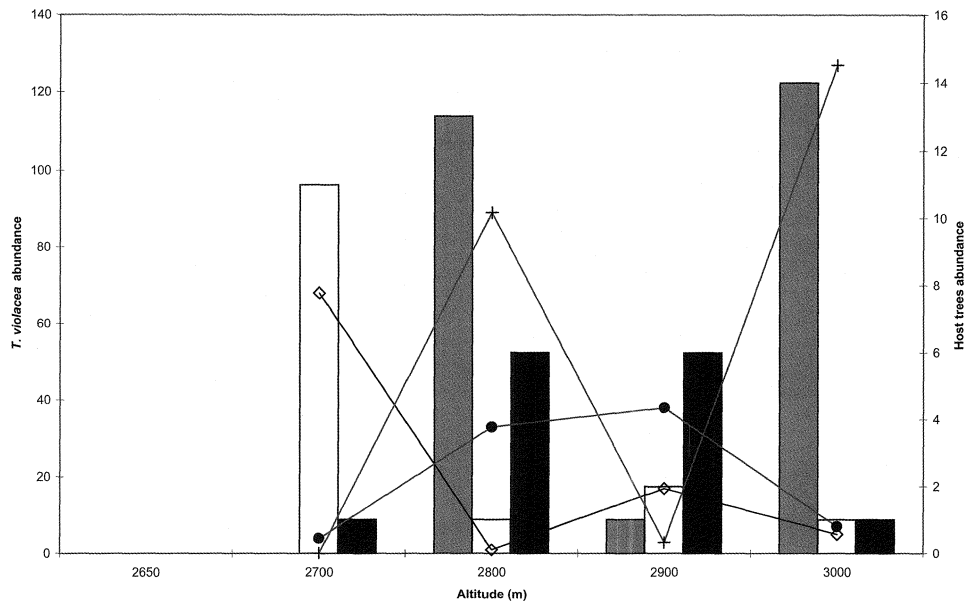


FIGURE 1. Abundance of *Tillandsia violacea* and abundance of host tree species along an altitudinal gradient in "El Chico" National Park, Hidalgo State, Mexico. ■, *Abies religiosa*; □, *Quercus rugosa*; ■, *Quercus laurina*; ◇, Epiphytes on *Q. rugosa*; ●, Epiphytes on *Q. laurina*; +, Epiphytes on *A. religiosa*.

altitude, we selected 20 *Quercus* spp. and 20 *Abies religiosa* trees. All trees had similar heights ( $16.45 \pm 3.52$  m). Individual *Tillandsia violacea* plants were counted in each tree, and the epiphyte position in the tree was recorded. Student's *t*-test was applied to compare the means of *T. violacea* abundance on *Quercus* spp. and *A. religiosa* trees (Zar 1984). Multivariate analysis of variance (MANOVA, Zar 1984) was used to evaluate significant differences between epiphytic plant numbers in each host tree species and among habitat classes. Data were transformed by  $\sqrt{x + 0.5}$  by normality when necessary.

## RESULTS

### Spatial Distribution Patterns

A total of 57 individual trees and 391 specimens of *Tillandsia violacea* was found in the four squares along the altitudinal gradient. The host tree species recorded were *Quercus rugosa* Née (14 individuals), *Q. laurina* Humb. et Bonpl. (15 individuals), and *Abies religiosa* Lindl. (28 individuals). Total tree density was  $633 \pm 184$  ind/ha (*Quercus* spp. =  $311 \pm 175$  ind/ha; *A. religiosa* =  $322 \pm 302$  ind/ha). The density of *Quercus* spp. in the study decreased with altitude, with maximum values at 2700 m altitude (533 ind/ha) and minimum values at

3000 m altitude (89 ind/ha). In contrast *Abies religiosa* density increased with altitude (FIGURE 1). The density of *T. violacea* on the host trees was  $6.9 \pm 4$  ind/tree ( $5.9 \pm 3.4$  ind/tree on *Quercus* spp. and  $7.8 \pm 4.4$  ind/tree on *A. religiosa*). The altitude effect was positive on *T. violacea* density, as we observed an exponential increase in the bromeliad density according to altitude ( $y = 0.2278e^{0.0012x}$ ;  $r_4 = 0.89$ ,  $P < 0.05$ , FIGURE 2).

The spatial pattern of distribution of *Tillandsia violacea* was clumped (TABLE 1). Morisita index analysis suggested a clumped pattern of distribution in the four habitat tree classes considered. Poisson analysis suggested a random pattern for branches, and the negative binomial distribution suggested a random distribution for the treetop base (TABLE 1).

The aggregation of *Tillandsia violacea* was related to host tree species and habitat class. Bromeliad frequency differed with each host tree species ( $H^2 = 19.2$ ;  $gl = 56$ ;  $P < 0.01$ ). Epiphytic plants were more frequently found on *Abies religiosa* trees (219 specimens of *T. violacea*) than on *Quercus* spp. (*Q. rugosa* = 90 plants; *Q. laurina* = 82 individuals). Nevertheless, along the altitudinal gradient, the abundance of *Quercus* trees decreased, and at 3000 m elevation and above, almost all trees present were exclusively *A. religiosa* (FIGURE 1).

No significant correlation between treetops

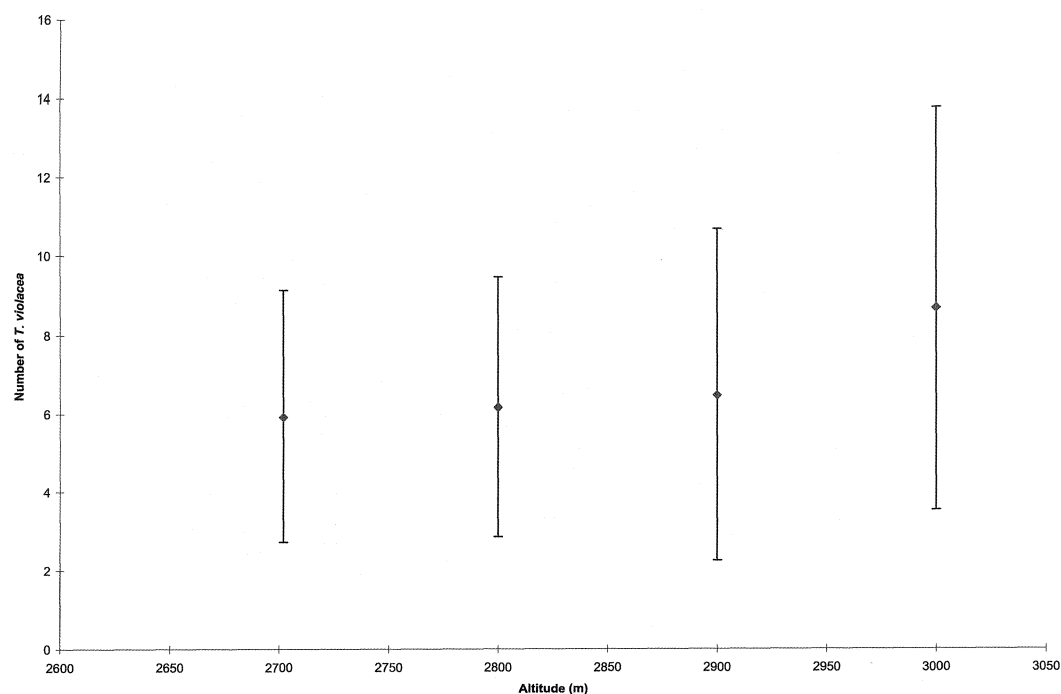


FIGURE 2. Mean of frequency of *Tillandsia violacea* per host tree along an altitudinal gradient in "El Chico" National Park, Hidalgo State, Mexico (lines indicate standard deviation).

and epiphyte abundance was obtained ( $r_{57} = 0.2$ ;  $P = 0.1$ ), perhaps because of the homogeneous size of *Abies religiosa* treetops.

Small branches were the preferred habitat of *Tillandsia violacea* (FIGURE 3). On the other hand, we found a significantly positive correlation between *T. violacea* abundance and the height of host trees ( $r_{57} = 0.60$ ,  $P < 0.0001$ ) (FIGURE 4). Such a correlation suggests that the preference could be related to the light tolerance of *T. violaceae*, which is considered to be a sun type (Benzing 1995).

#### Support Tree Preferences

We found a larger individual number of *Tillandsia violacea* on *Abies religiosa* (150 plants:  $8 \pm 3$  epiphytes/tree) than on *Quercus* spp. (109

plants:  $5 \pm 3$  epiphytes/tree). Student's *t*-test indicates significant differences between means of epiphyte abundances ( $t_{0.05,38} = 2.1$ ;  $P = 0.02$ ).

Data for the effect of habitat class on the sampling species tree are presented in TABLE 2. The analysis (MANOVA) suggested no significant effect of host tree species on epiphyte abundance, while habitat class and interaction between factors had a significant effect. The post hoc analysis (Tukey test) suggested differences in epiphyte numbers on the trunks of *Quercus* spp.

#### DISCUSSION

Epiphyte density in our study area ( $0.44$  ind/ $m^2$ ) was higher than that reported in tropical forests of Venezuela,  $0.05$  ind/ $m^2$ , including hemi-

TABLE 1. Spatial distribution pattern analysis of *Tillandsia violacea* in the different habitat classes on phorophyte species studied in "El Chico" National Park (\* =  $P < 0.001$ ; \*\* =  $P < 0.05$ ).

Habitat class	Poisson	Negative binomial	Morisita
Trunk	Clumped*	Clumped*	Clumped*
Treetop	Clumped**	Random**	Clumped*
Branches	Random	Clumped*	Clumped*
Small branches	Clumped*	Clumped*	Clumped*

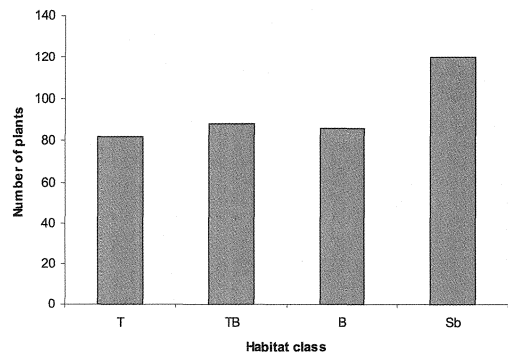


FIGURE 3. Number of plants of *Tillandsia violacea* found in the four habitat classes selected on host tree species studied in "El Chico" National Park, Hidalgo State, Mexico. (T = trunk; TB = treetop base; B = branches; Sb = small branches).

epiphytes (Nieder et al. 2000). Nevertheless, Bøgh (1992) found highest epiphyte density in montane forest of Ecuador, at 2900 m altitude (20 ind/m<sup>2</sup>). Differences in densities can be attributable to lack of substrate for establishment of epiphytes, related with factors such as tree bark characteristics (Nieder et al. 2000); scarcity of bryophytes that modified the substratum characteristics allowing colonization by other epiphytic plants (Benzing 1980); and precipitation patterns and altitude that influenced humidity and dry periods for epiphytic communities (Sug-

den & Robins 1979). Finally, epiphyte diversity in the community is beneficial, as different species could grow on different habitats in the forest landscape (Flores-Palacios & García-Franco unpubl. data). The latter factors interrelating with host tree availability (tree density, size, and architecture) could explain the epiphyte densities found.

Our results show an increase of epiphyte density with altitude; the highest bromeliad abundance was found at 2800–3000 m. On those study sites, we also recorded the highest number of host trees and an abundance of bryophytes.

Some authors propose that density and biomass of epiphytic plants tend to increase with altitude in different vegetation types (Nadkarni 1984, Ingram & Nadkarni 1993, Freiberg 1999). Other studies, however, show the opposite trend, with epiphyte biomass remaining constant through an altitude gradient (García-Franco & Peters 1987, Freiberg & Freiberg 2000). Differences in the influence of altitude on density and biomass of epiphytic plants have been related to surrounding vegetation and climatic conditions of studied areas (Vandunné 2002). Altitude influences epiphytic strategies to resolve space, nutrient, and humidity requirements.

Related to these environmental requirements of epiphytic plants, we found a trend of preference for some host tree species. The largest number of epiphytes was recorded on *Abies religiosa*, which are usually taller than *Quercus*

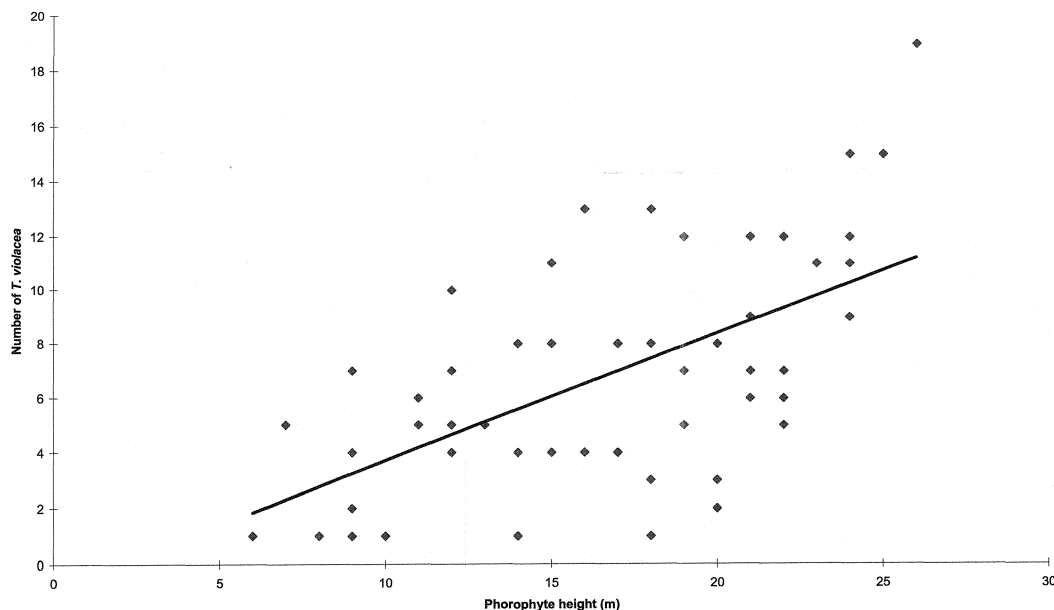


FIGURE 4. Relationship between phorophyte height and *Tillandsia violacea* abundance in "El Chico" National Park, Hidalgo State, Mexico.

TABLE 2. Abundance of *Tillandsia violacea* on *Quercus* spp. and *Abies religiosa* trees in the four habitat classes studied ( $N = 40$ ).  $F$  values ( $P < 0.05$  = significant). Different letters in the same row show significant statistical differences in accordance with Tukey's test ( $P < 0.005$ ); df = degrees freedom for  $F$ -test statistic used to determine significance of effect; MS = mean squares of effect.

Host tree species	Trunk	Treetop base	Branches	Small branches
<i>Quercus</i> spp.	19 <sup>a</sup>	30 <sup>b</sup>	27 <sup>b</sup>	33 <sup>b</sup>
<i>Abies religiosa</i>	46 <sup>a</sup>	30 <sup>a</sup>	31 <sup>a</sup>	43 <sup>a</sup>
Factor	MS	df	$F$	$P$
Host species	7.66	1,152	2.66	0.10
Habitat class	51.97	3,152	18.03	0.00005
Interaction	39.96	3,152	13.86	0.00005

trees and which offer an extensive surface area to the epiphytes. The correlation between host tree height and epiphyte abundance was significant (FIGURE 4), suggesting that tree height is a significant parameter in establishment of epiphytes on the trees.

Studies made in Costa Rica demonstrated positive correlations between treetops size and epiphyte abundance (Yeaton & Gladstone 1982). We did not find such a relationship. Studied trees, particularly *Abies religiosa*, had homogeneous treetops, because we selected trees of similar height and because of the allometric relation between tree height and treetop area. The size and form of *Abies* canopies provide an environment for the establishment of more epiphytic seeds, in contrast to *Quercus* leaves, which are larger and wider and thus obstruct windblown seed.

On other hand, differences were found in the availability of organic matter accumulated in bromeliad tanks, depending on the leaf structure of host trees (Castaño-Meneses 2002). *Abies religiosa* leaves are more easily introduced and accumulated in bromeliad tanks than are those of *Quercus* spp. Host tree leaf size has a major effect on the decomposition process and nutrient release in *Tillandsia violacea* (Castaño-Meneses 2002). The amount of accumulated debris in *A. religiosa* is twice that recorded in *Quercus* spp.

Our results showing a clearly clumped spatial distribution pattern of *Tillandsia violacea* are similar to studies of epiphyte distribution in other locations (Sugden & Robins 1979, Nieder et al. 2000, Vandunné 2002). This pattern is associated with limited dispersion mechanisms, as evidenced by the frequency of juveniles close to reproductive plants (Madison 1979). Host tree distribution and epiphyte distribution, together with canopy microhabitat, however, influence horizontal and vertical epiphytic distribution in forest canopies (Vandunné 2002).

We found a positive effect of altitude on *Tillandsia violacea* abundance, with variations in

host tree distribution and most extensive use of *Abies religiosa* as a support tree, which is most abundant at the highest elevations.

#### ACKNOWLEDGMENTS

J. Monterrubio assisted with fieldwork. V. Rico-Gray, Z. Cano, H. Brailovsky, A. García-Aldrete, and S. Zaragoza provided valuable suggestions on the first draft. Two anonymous reviewers made useful comments for improving the manuscript, and Lawrence Ross reviewed the manuscript for spelling. This research constitutes partial fulfillment of the senior author's Ph.D. program at Facultad de Ciencias, UNAM.

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## FLOWER BIOLOGY OF SIX CULTIVARS OF THE BROMELIACEAE I. POLLEN, PISTIL, AND PETAL APPENDAGES

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**ABSTRACT.** The authors determined morphometric data of different floral features and in vitro pollen germination of six cultivars representing four genera and two subfamilies of Bromeliaceae. Important floral characteristics for plant breeding are pollen germination and style length. Pollen viability was for all cultivars more than 40% and high enough for successful pollination. Stylar length varied much for the different cultivars. Scanning electron microscopy (SEM) was used to examine important flower characteristics. The pollen of *Aechmea fasciata* were biporate, and those of *Tillandsia cyanea*, *Vriesea* × *viminalis*-*rex* × *carinata* and *V. splendens* were monosulcate. Pollen grains of *A. chantinii* and *Guzmania lingulata* were inaperturate. The exine layers of all taxa were reticulate in structure with the exception of *A. chantinii*, which was smooth. Four stigma types were detected: convolute-blade, conduplicate-spiral, simple-erect, and coralliform. Petal appendages of *Vriesea* were tongue-like and absent in *G. lingulata* and *T. cyanea*. *Aechmea fasciata* and *A. chantinii* had complex petal appendages. Ovules of all cultivars possessed characteristic chalazal appendages.

**Key words:** Bromeliaceae, ovary, ovules, petal appendages, pollen, stigma

### INTRODUCTION

Bromeliaceae are predominantly neotropical epiphytic herbs or terrestrial xerophytes comprising about 62 genera and 2800 species (Smith & Downs 1974, Benzing 1980, W. Till unpubl. data). Bromeliads tend to be ornamental and are easy to cultivate. In spite of the size of the family and its horticultural importance, little is known about the floral architecture and reproductive biology (Gilmartin & Brown 1986, Benzing 2000). The family is traditionally divided into three subfamilies: Pitcairnioideae, Tillandsioideae, and Bromelioideae (Smith & Downs 1974, 1977, 1979). Pitcairnioideae and Tillandsioideae have mostly hypogenous flowers, and the fruits are capsules. Bromelioideae have epigenous flowers and baccate fruits (Benzing 1980, Dahlgren et al. 1985). The flower structure of bromeliads is neither primitive nor highly evolved. The flowers are mostly bisexual and basically three-parted; there is a three-chambered ovary topped by a style with a three-lobed stigma. Three petals alternate with an equal number of smaller sepals. The six stamens (usually) are positioned in two whorls of three each (Benzing 1980, 2000). Bromeliads, like most monocots have a hollow (open) style. The ovules are anatropous, bitegmic, and crassinucellate with the micropyle formed by the inner integument (Davis 1966, Johri et al. 1992). Bromeliads have wet stigmas with a low to me-

dium amount of specialized glandular cells, the papillae (Heslop-Harrison & Shivanna 1977, Knox et al. 1986).

Brown and Gilmartin (1989) studied more than 400 Bromeliaceae for stigma morphology. Five types account for all known variation. Small paired or single outgrowths from the base of each petal, known as petal appendages are common in Bromeliaceae and are most probably involved in intrafloral nectar management (e.g., nectar retention, presentation, and delivery) (Brown & Terry 1992). An important taxonomic aspect is pollen grain appearance (Halbritter 1992). The most significant diagnostic features of pollen grains are their size, shape, apertures (germination pores), and exine surface structure (Shivanna & Rangaswamy 1992). Pollen viability indicates the ability of the pollen grain to deliver sperm cells to the embryo sac following compatible pollination (Shivanna et al. 1991, 1997). Tests for germination capacity and normal pollen tube growth on in vitro media provide a direct and reliable assessment of viability (Heslop-Harrison et al. 1984). Pollen of many plant species, typically binucleate pollen, germinates and grows well in culture. Bromeliaceae have binucleate pollen (Brewbaker 1967, Johri et al. 1992).

The goal of this study was to present a survey on flower characteristics: morphometric data, stigma type, papillae, petal appendages, pollen grain, and ovule morphology of six economically and horticulturally important cultivars. Most studies on bromeliad flower morphology deal

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